

The *Stenoplax limaciformis* (Sowerby, 1832) Species Complex in the New World (Mollusca: Polyplacophora: Ischnochitonidae)

by

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Abstract. The systematic status of species traditionally associated with the *Stenoplax limaciformis* species complex of the New World has remained controversial. The group is reviewed and four sibling species are recognized on the basis of differences in shell sculpture, radular morphology, and esthete pore density: *Stenoplax limaciformis* (Sowerby, 1832) from the tropical eastern Pacific, *S. purpurascens* (C. B. Adams, 1845) from the West Indies and northern South America, *S. floridana* (Pilsbry, 1892) from the Florida Keys south to Colombia, and a long-neglected species, *S. producta* (Reeve, 1847), from the Bahama Islands, Cuba, Jamaica, and Hispaniola south to Honduras and Isla de San Andrés. Two distinct lineages are recognized within the sibling group: (1) *S. floridana* and *S. producta* from the western Caribbean and (2) the West Indian *S. purpurascens* and the eastern Pacific *S. limaciformis*. The restricted distribution of the Caribbean species within the West Indian Faunal Province, which is assumed to be a result of a very brief free-swimming larval stage, the insular environment of the area, and ocean current patterns, lends support to the theory of paraprovincialism as applied to the Caribbean. *Stenoplax floridana* and *S. producta* exhibit a Caloosahatchian distributional pattern, while *S. purpurascens* reflects a Gatunian origin.

INTRODUCTION

THE CONFUSING nomenclatural history of *Stenoplax limaciformis* (Sowerby, 1832) and the related nominal species *S. purpurascens* (C. B. Adams, 1845) and *S. floridana* (Pilsbry, 1892) has been presented by KAAS (1972) and FERREIRA (1978). Taxonomic problems exist due to limited material available for study, intraspecific variability, and the small, but consistent, differences exhibited by these species. The untrained eye, even with the aid of a dissecting microscope, may not easily differentiate the species of *Stenoplax*.

During the first half of this century two species within the *Stenoplax limaciformis* group were recognized: *S. limaciformis* from the eastern Pacific and the West Indies, and *S. floridana* from the Florida Keys. KAAS (1972), on the basis of limited and poorly preserved material, concluded that the West Indian populations of "*limaciformis*" represent a distinct species, *S. purpurascens*. ABBOTT (1974) recorded all three species from Florida and the West Indies. After an examination of large samples of these nominal species, FERREIRA (1978) concluded that all of these

Stenoplax "species" are, in fact, a single biological species. In the most up-to-date listing of Recent polyplacophoran species, KAAS & VAN BELLE (1980) supported Ferreira in part, and they synonymized *S. purpurascens* with *S. limaciformis*; however, they retained *S. floridana* as a distinct species. I will show in the present study that the *S. limaciformis* complex must be considered as a group of sibling species. Each of the previously mentioned species is specifically distinct and, furthermore, a fourth species, *S. producta* (Reeve, 1847), also exists in the Caribbean region.

MATERIALS AND METHODS

Specimens from the Museum of Comparative Zoology (Cambridge), the Florida Department of Natural Resources Marine Research Laboratory, and the personal collections of G. T. Watters (Ohio State University) and the author were examined in detail. Other material was available due to the kindness of A. Solem of the Field Museum of Natural History, T. Hopkins and D. Blizzard of the Dauphin Island Sea Lab, J. Brooks, D. Dexter, D.

Holt, A. Martins, and T. Spight. Photographs of previously examined type material in the British Museum (Natural History) and the Museum National d'Histoire Naturelle, Paris, were available for study.

Only non-eroded specimens were used for the various aspects of this study. Dry specimens most easily revealed the small sculptural features necessary for species determination; preserved or living specimens were blotted with an absorbent wipe to remove surface liquid.

The shell-plates (valves) of many individuals were disarticulated and cleaned using a 2 N solution of KOH. Specimens to be studied using scanning electron microscopy (SEM) were further cleaned in heated KOH solution and then placed in a series of distilled water rinses during which they were ultrasonically cleaned. The valves were then mounted on aluminum specimen stubs using Duco cement and wedges of aluminum foil. After coating with carbon and gold/palladium in a Denton DV-502 vacuum evaporator, the samples were studied using an ISI SEM model MSM-3, located in the Department of Zoology at the University of Rhode Island.

Examination of numerous SEM photographs revealed apparent differences in esthete pore density that showed promise for phylogenetic studies. For this part of the investigation a total of 41 individuals was selected at random. Examples of *Stenoplax limaciformis* came from Mexico (n = 3) and Panama (n = 10); *S. purpurascens* from Puerto Rico (n = 1), the Dominican Republic (n = 1), Barbados (n = 1), Aruba (n = 1), and Panama (n = 7); and *S. floridana* from the Florida Keys (n = 8), Honduras (n = 1), and Panama (n = 2). For each individual, SEM photographs of an intermediate valve were made of the top central area (TC), anterior margin (AM), and lateral triangle (LT). Each photograph covered 0.145 mm² of the shell surface. Surface area measurements and esthete pore counts were taken from 20.3 × 25.4 cm photographic enlargements. In all TC calculations any portion of the lateral triangle that was visible was excluded from consideration. All area measurements were made using a K & E compensating polar planimeter. In order to ascertain the phylogenetic usefulness of these data, percent rib area (PCTRA), a measure of rib prominence, was plotted against micropore density (SDEN), megalopore density (LDEN), and total pore density (TOTDEN) for each area of the valve. It was evident that LDEN, which represents the density of megalesthetes, was a more meaningful character than SDEN due to the high degree of variability in the number of microesthetes associated with each megalesthete. Further analyses involved only LDEN for the three areas of the intermediate valve combined.

Canonical variate analysis, using LDEN and PCTRA as variables, was employed in order to examine the differences between the species that were established *a priori* on the basis of general shell and radular features. Mahalanobis D² distances were calculated for each pair of species. In canonical variate analysis, variables are transformed to maximize differences between *a priori* groups

relative to within group variation (NEFF & MARCUS, 1980; CAMPBELL & ATCHLEY, 1981). This form of analysis has been shown to be an invaluable tool in the analysis of variation between populations, groups of populations, and species. All computations were carried out using the SAS program at the Academic Computer Center at the University of Rhode Island.

The valves selected for line drawings were taken from individuals used for SEM studies. These valves were mounted on large pins and coated with magnesium oxide in order to enhance sculptural detail.

Radulae and girdle elements were briefly examined using SEM techniques; however, most samples were more easily studied using light microscopy. Permanent microslide mounts were prepared by dehydrating in ethanol, clearing in toluene, and mounting in Canada balsam.

The radulae were excised, thoroughly cleaned, and teased apart before study. The many small differences noted in denticle cap morphology were best seen in an outline view of the cap; for each preparation a portion of the radula was teased apart enough to separate some denticle caps from major lateral teeth. In specimens that had been preserved for more than a few years, this posed no substantial problem because there was a tendency for the denticle caps to fall off during the cleaning stages. The caps, due to their magnetic property, were collected on the tip of an insect pin and transferred to the mounting medium. The radulae of 69 individuals were examined in detail by light microscopy (*Stenoplax limaciformis*, 6; *S. purpurascens*, 7; *S. floridana*, 29; *S. producta*, 27). The radulae of 139 other individuals were isolated, cleaned, and observed, but not mounted.

Girdle scales were studied using cleaned, isolated scales. Because of the great amount of variation between girdle scales, the marginal spicules, and the small ventral scales of the same specimen, preparations were made by taking a small sample (about a fourth of the animal length, on one side in the middle) and processing it as a unit. The scales often separated, especially during ultrasonic cleaning, but they were pipetted and transferred to a microslide using a small, disposable Pasteur pipet. The scales were allowed to settle in the pipet in order to concentrate them. The filmlike folded sheet of ventral scales and the remainder of the dorsal scales were then added to the slide before the Canada balsam was applied. The small, rectangular scales of the ventral surface of the girdle were so similar among the species examined that descriptions of them are not included in the present study. Therefore, all references to "girdle scales" refer to the dorsal scales and the outer fringe of spicules.

ABBREVIATIONS

The following institutions and individuals are cited in the text using the abbreviations listed below:

ANSP—Academy of Natural Sciences of Philadelphia
BLM—Bureau of Land Management

BMNH—British Museum (Natural History), London
 DISL—Dauphin Island Sea Lab, Alabama
 FDNR—Florida Department of Natural Resources Marine Laboratory, St. Petersburg
 FMNH—Field Museum of Natural History, Chicago
 GTW—Collection of G. T. Watters
 MCZ—Museum of Comparative Zoology, Cambridge
 MNHNP—Museum National d'Histoire Naturelle, Paris
 RCB—Collection of R. C. Bullock
 SDSC—San Diego State College

SYSTEMATIC SECTION

Family ISCHNOCHITONIDAE Dall, 1889

Subfamily ISCHNOCHITONINAE Dall, 1889

The systematics of polyplacophorans at the family and subfamily levels are greatly in need of revision. I follow the conservative approach presented by KAAS & VAN BELLE (1980), who included in the Ischnochitoninae the genera *Ischnochiton* Gray, 1847, *Stenoplax* Dall, 1879, *Stenochiton* H. Adams & Angas, 1864, *Lepidozonia* Pilsbry, 1892, and *Connexochiton* Kaas, 1979. The only recent review of the subfamily is that of VAN BELLE (1977).

Genus *Stenoplax* (Carpenter MS) Dall, 1879

Type species: *Chiton limaciformis* Sowerby, 1832 by original designation.

There is a difference of opinion concerning the authorship of *Stenoplax* and other names proposed in the large unpublished chiton manuscript of P. P. Carpenter and later properly introduced by DALL (1879), PILSBRY (1892–1894), and others. SMITH (1960), KEEN (1971), FERREIRA (1978), and various west coast workers have consistently assigned authorship to Carpenter. DALL (1879) and PILSBRY (1892–1894) credited Carpenter where they took information directly from the manuscript. The manuscript, housed in the Division of Mollusks at the U.S. National Museum of Natural History, is in two large scrapbooks. Much of the writing is in curious shorthand. Given the condition of the manuscript, it seems to me incredible that Carpenter should be considered as having published these names in the meaning of the International Code of Zoological Nomenclature. I follow BOSS *et al.* (1968) and assign the authorship to the person who validly introduced the name in question.

The genus *Stenoplax* was introduced (DALL, 1879:78) on the same page as *Stenoradsia*. The latter name is currently accepted as a subgenus of *Stenoplax s.l.* (SMITH, 1961; VAN BELLE, 1977; KAAS & VAN BELLE, 1980). SMITH (1961) also listed *Stenochiton* Adams & Angas, 1864, as a subgenus of *Stenoplax*, but Australian workers (*cf.* ASHBY, 1918; IREDALE & HULL, 1927) and VAN BELLE (1977) have considered *Stenochiton* a separate genus. Should this genus of elongate, *Stenoplax*-like chitons be considered congeneric with *Stenoplax*, the name *Stenochiton* would have precedence.

When DALL (1879) introduced the genus *Stenoplax*, he listed the type species as "*S. limaciformis* Sby." It seems inconceivable that Dall, or Carpenter who had no doubt seen type specimens in the British Museum, could have misidentified such a well known species; but the only information presented by Dall, including his figure (pl. 2, fig. 13), does not coincide with features of *S. limaciformis* or any other *Stenoplax s.s.* Dall stated that the central tooth is very small and that the major lateral tooth has a simple cusp. In fact, all *Stenoplax s.s.* have a tricuspidate denticle cap (THIELE, 1893; TAKI, 1954; this paper), and the central tooth is moderately narrow but certainly not "small" as Dall stated. In spite of this discrepancy, the use of the name *Stenoplax* has not been questioned.

Stenoplax Dall *s.s.*

Description: Animal elongate, of medium size, reaching a length of about 50 mm. Color highly variable. Valves moderately flattened to inflated. Sculpture of anterior valve and posterior slope of posterior valve granular, nodulose, or of concentric ribs; in some forms the granules or nodules coalesce to form radial or concentric sculpture. Central areas and jugum with longitudinal ribs which may break up into pustules near the lateral triangle. Mucro of posterior valve central or posteriorly acentric. Slitting of insertion plates highly variable within each species; anterior valve with 8–14 slits, posterior valve with 7–12 slits; intermediate valves with one slit per side. Dorsal girdle scales very small, typically about 120 μ m high, 80 μ m wide, with 9–19 ribs per scale; ribs may or may not reach apex. Denticle cap of major lateral tooth tricuspidate.

Stenoplax s.s. includes: *S. limaciformis* (Sowerby, 1832) from the eastern Pacific; *S. purpurascens* (C. B. Adams, 1845), *S. floridana* (Pilsbry, 1892), and *S. producta* (Reeve, 1847) from the western Atlantic; and *S. venusta* (Is. & Iw. Taki, 1931) and *S. alata* (Sowerby, 1841) from the Indo-Pacific region. *Ischnochiton kempfi* Righi, 1971, from Brazil is also a *Stenoplax*, but KAAS & VAN BELLE (1980) considered it a member of the subgenus *Stenoradsia*; its relationship to *Stenoplax s.s.*, especially the *S. floridana*–*S. producta* lineage, needs to be investigated, but material is presently unavailable. Some other New World species may be properly placed in *Stenoplax s.s.* For example, *S. boogi* (Haddon, 1886) appears to be a *Stenoplax*, but it does not belong to the *S. limaciformis* group. ABBOTT (1974) included *Ischnochiton erythronotus* (C. B. Adams, 1845) in *Stenoplax*, but FERREIRA (1978) noted that this species is a junior subjective synonym of *Ischnochiton striolatus* (Gray, 1828) which is not considered a *Stenoplax*.

I have found that the girdle scales of *Stenoplax s.s.* polarize light. Whether there is any adaptive significance to this crystalline structure of calcium carbonate is unknown.

The biology of *Stenoplax s.s.* species is poorly known. Anatomical observations were reported by PLATE (1901) who studied *S. alata* from the Philippine Islands. It is generally thought that polyplacophorans are herbivorous

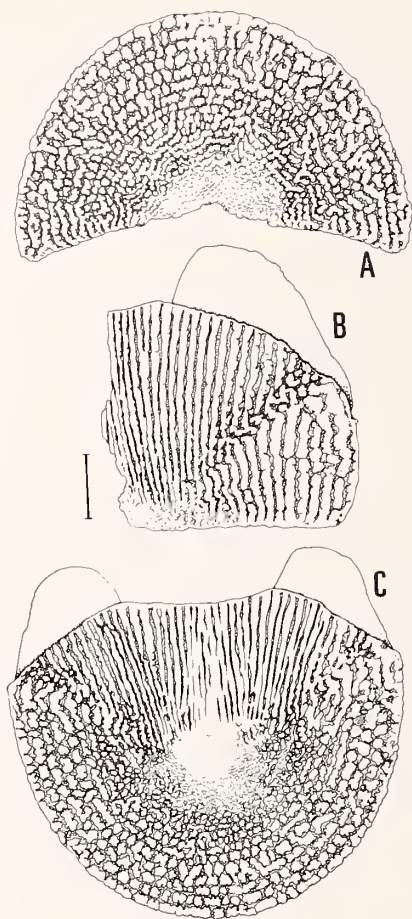


Figure 1

Stenoplax limaciformis (Sowerby). Punta Mala, Panama (RCB). A, anterior valve. B, right portion of intermediate valve. C, posterior valve. Scale bar = 1 mm.

(HYMAN, 1967), but some chitons are definitely omnivorous if not carnivorous (BARNAWELL, 1960; MCLEAN, 1962; Thorpe in KEEN, 1971). *Stenoplax* appears to fall into the latter category. PLATE (1901) found foraminiferans in the gut of *S. alata*. RAEHLE (1967) reported that aquarium-kept *S. floridana* feed on mussel meat.

Stenoplax s.s. lives in a fairly restricted habitat. In a note on a label for *S. limaciformis*, a collector noted that it was found living "buried on sides of deeply bedded rocks." Caribbean species also live on rocks embedded in the substrate. In all cases, the rocks must actually be embedded, not just be resting on other rocks, and the substrate is usually clean, coarse sand or gravel. The species are absent in silty areas or in anaerobic substrates. Species of *Stenoplax s.s.* typically inhabit shallow waters from the low tide mark to a depth of a few meters. They are known to occur in deeper water as records from the western coast

of Florida and the Bahamas attest. RIGHI (1971) obtained specimens of *S. purpurascens* from as deep as 90 m.

Key to the species of the
Stenoplax limaciformis species complex

1. Ribs of central areas conspicuously broken into pustules near lateral triangle; lateral triangle usually granular *S. floridana*
Ribs of central areas forming few, if any, pustules; lateral triangle with concentric ribs which may be broken into broad nodules 2
2. Posterior valve elongate; mucro posteriorly acentric; microfurrows, visible under high magnification, in all grooves *S. producta*
Posterior valve not elongate; mucro centrally located; grooves smooth 3
3. Anterior valve and posterior slope of posterior valve with wavy, concentric ribs *S. purpurascens*
Anterior valve and posterior slope of posterior valve with nodular sculpture *S. limaciformis*

Stenoplax limaciformis (Sowerby, 1832)

(Figures 1–7, 8A, B, 9A)

Chiton limaciformis Sowerby in BRODERIP & SOWERBY, 1832: 26 (Inner Lobos Island in Peru and Guacomayo in Central America; holotype in BMNH); REEVE, 1847: pl. 8, sp. 42.

Chiton (Ischnochiton) limaciformis Sowerby. SHUTTLEWORTH, 1853:190.

Stenoplax limaciformis (Sowerby). DALL, 1879:78; KEEN, 1958:526, fig. 44; Thorpe in KEEN, 1971:871, sp. 24; ABBOTT, 1974 [in part]:396; FERREIRA, 1978 [in part]: 87; KAAS & VAN BELLE, 1980:74.

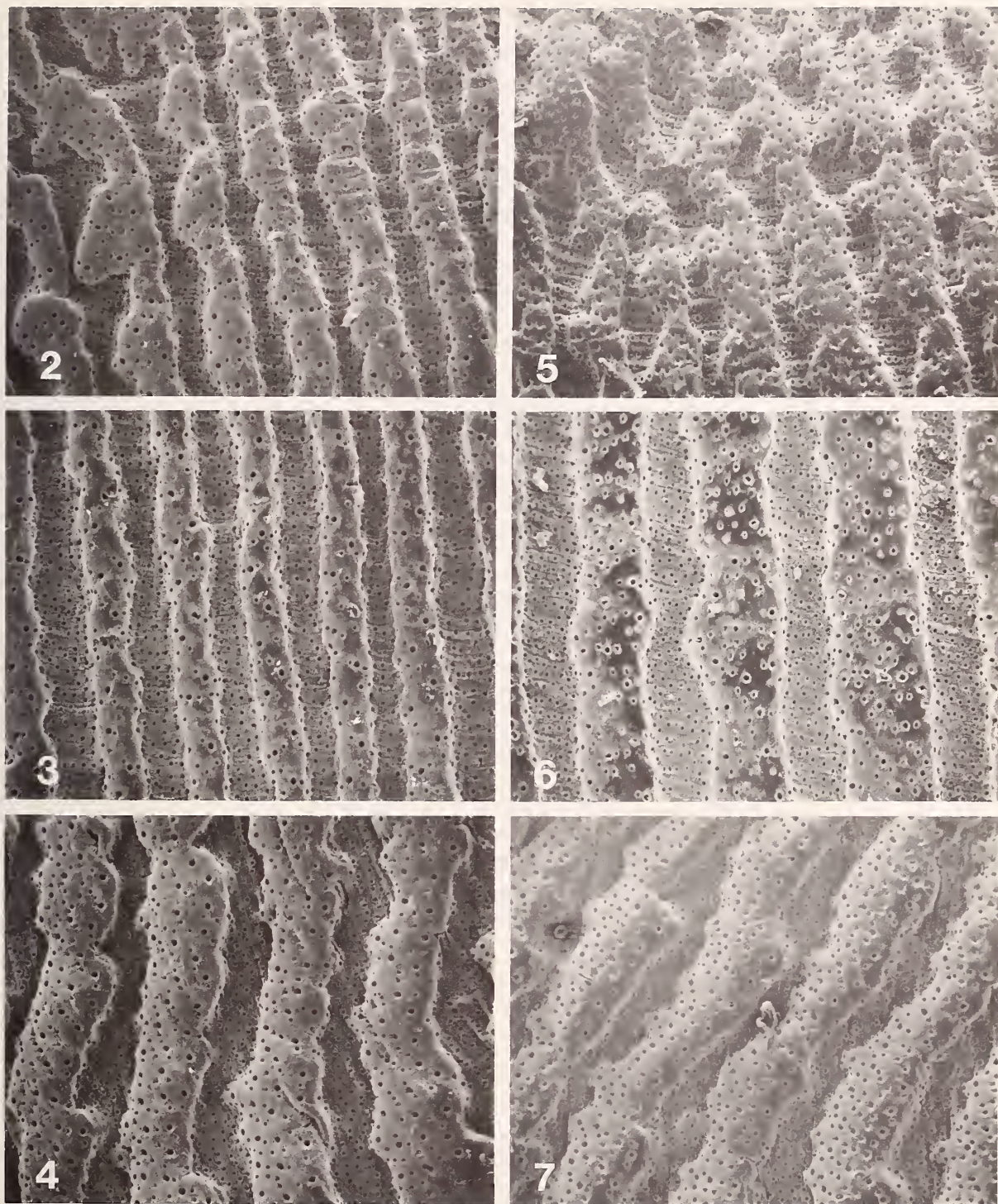
Ischnochiton (Stenoplax) limaciformis (Sowerby). PILSBRY, 1892:57, pl. 16, figs. 9–16.

Chiton angustus CLESSIN, 1904:120, pl. 41, fig. 1 (Central America; location of type unknown).

Ischnochiton limaciformis (Sowerby). PILSBRY & LOWE, 1932: 129; KAAS, 1972:71.

Description: Animal reaching a length of 45 mm, elongate. Anterior valve with concentrically arranged nodules, but occasionally nodules coalesce to form radially arranged groups of nodules; insertion plate with 9–13 slits. Intermediate valves rounded; longitudinal ribs of central area about as wide as intervening grooves and bend laterally; ribs become irregular near lateral triangle; ribs of jugum close-packed. Lateral triangle with broad close-packed concentric ribs which at times are broken to give a slightly nodular appearance. One slit per side in insertion plate. Posterior valve with central mucro; central areas with sculpture like that of intermediate valves; posterior slope sculpture similar to that of anterior valve; insertion plate with 7–12 slits.

Girdle scales slightly curved, variable in proportions, but typically about 102 μm long, 87 μm wide; 10–19 ribs per scale; ribs reach apex. Girdle fringe with straight, ribbed spicules, approximately 120 μm in length.



Explanation of Figures 2 to 7

Scanning electron micrographs of intermediate valve sculpture of *Stenoplax limaciformis* (Sowerby). Posterior side toward top of page; all photographs 186 \times . Figures 2 to 4: Punta Mala, Panama (RCB). Figures 5 to 7: Acapulco, Mexico (MCZ 204170).

Figures 2, 5. Posterior region of central area near lateral triangle. Note the large number of esthete pores on the ribs, the lack of groove microsculpture, and that the ribs become irregular, but that they do not break into pustules.

Figures 3, 6. Central area near anterior margin.

Figures 4, 7. Lateral triangle.

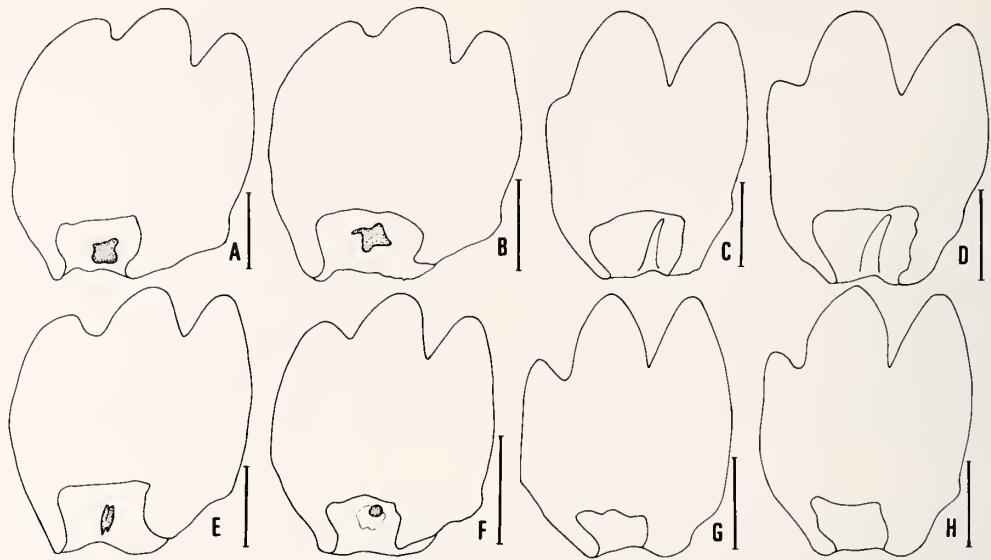


Figure 8

Representative denticle caps of the major lateral radular tooth of New World species of the *Stenoplax limaciformis* complex.

A and B, *S. limaciformis*: A, Playa Caleta, Acapulco, Mexico (RCB); B, Punta Mala, Panama (RCB).

C and D, *S. producta*: C, Anthony's Key, Roatán Id., Honduras (RCB); D, Harbour Island, Eleuthera, Bahama Islands (GTW).

E and F, *S. purpurascens*: E, Bridgetown, Barbados (RCB); F, North side of Galeta Id., Panama (RCB).

G and H, *S. floridana*: G, Verde Id., Mantilla Pt., Porto Bello, Panama (RCB); H, Indian Key Fill, Florida Keys, Florida (RCB). Scale bar = 50 μ m.

Radula typical for subgenus. Denticle cap of major lateral tooth tricuspidate, rather squat; small cusp moderately pronounced; side with small cusp swollen; brown basal spot present.

Remarks: *Stenoplax limaciformis* seems to be most closely related to *S. purpurascens*. Both species have blunt cusps and a brown basal spot on the denticle cap, and both exhibit rather broad ribs with many esthete pores on the central areas. Neither species has any break-up of the central area ribs into pustules. The more even, wavy, concentric ribs of the anterior valve and the posterior slope of the posterior valve separate *S. purpurascens* from *S. limaciformis*. The denticle caps of the two species are quite different: in *S. purpurascens* the small cusp is much more pronounced than in *S. limaciformis*, and the outline of the denticle cap on the side of the small cusp is never swollen as it always is in *S. limaciformis* (Figures 8A, B, E, F). For additional comments about the relationship between *S. limaciformis* and *S. purpurascens*, see the remarks for the latter species.

Distribution: *Stenoplax limaciformis* occurs from Puerto-citos and La Libertad, Mexico, south to Peru (Thorpe, in KEEN, 1971) (Figure 9A).

Specimens examined: *Mexico:* San Luis Gonzaga; Mazatlán (both MCZ); Isla Pajaros, Mazatlán (SDSC); Acapulco (MCZ, RCB).—*Costa Rica:* Playas del Coco [10°31'N, 85°43'W] (RCB).—*Panama:* Punta Mala; Naos Id.; Culebra Id.; W side of Taboga Id.; W side of Morro de Taboga, Taboga Id.; E side of Taboga Id., near Urava Id. (all RCB).

Stenoplax purpurascens (C. B. Adams, 1845)

(Figures 8E, F, 9A, 10–13)

Chiton purpurascens C. B. ADAMS, 1845:9 (Jamaica; holotype MCZ 155962); CLENCH & TURNER, 1950:334, pl. 42, fig. 2 [holotype figured].

Chiton sanguineus REEVE, 1847:pl. 17, sp. 98 (St. Vincent, W. Indies, holotype in BMNH).

Chiton (Ischnochiton) purpurascens C. B. Adams. SHUTTLEWORTH, 1853:199.

Onitochiton [sic] pruinusum ROCHEBRUNE, 1884:35 (Ile Cochino, Guadeloupe; type in MNHNP).

Ischnochiton (Stenoplax) limaciformis (Sowerby). DALL, 1889: 415 [in part]. *Non Stenoplax limaciformis* (Sowerby).

Ischnochiton limaciformis (Sowerby). PILSBRY, 1892:57 [in part]; DALL & SIMPSON, 1901:452; WARMKE & ABBOTT, 1961:217, text fig. 32e; RIGHI, 1971:126, figs. 13–18; GÖTTING, 1973:248, pl. 9, fig. 5; RIOS, 1975:265;

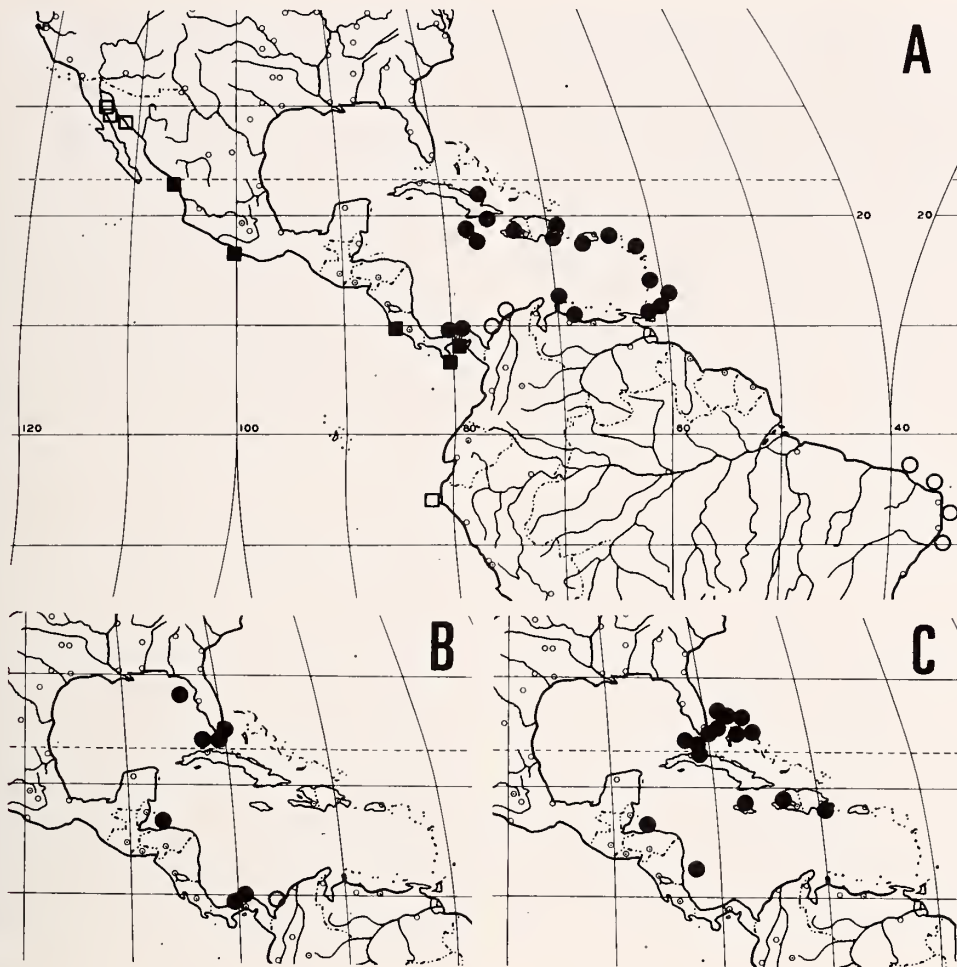


Figure 9

Known distribution of species of the *Stenoplax limaciformis* complex in the New World. A, *S. limaciformis* (■) and *S. purpurascens* (●). B, *S. floridana*. C, *S. producta*. Closed marks represent specimens examined; open marks indicate localities taken from the literature.

HUMFREY, 1975:290, fig. 18d. *Non Stenoplax limaciformis* (Sowerby).

Stenoplax producta (Reeve). THIELE, 1909:7. *Non Stenoplax producta* (Reeve).

Ischnochiton productus (Reeve). THIELE, 1910a:80; THIELE, 1910b:110. *Non Stenoplax producta* (Reeve).

Ischnochiton purpurascens (C. B. Adams). ABBOTT, 1954:320; ABBOTT, 1958:108.

Stenoplax purpurascens (C. B. Adams). ABBOTT, 1974:396 [erroneously reported from the Florida Keys and Bermuda].

Stenoplax limaciformis (Sowerby). FERREIRA, 1978 [in part]:87; KAAS & VAN BELLE, 1980 [in part]:74. *Non Stenoplax limaciformis* (Sowerby).

valves often streaked or speckled with darker or lighter colors. Anterior valve with broad, close-packed, wavy, concentric ribs; insertion plate with 9–13 slits. Intermediate valves somewhat flattened to quite inflated; ribs of central areas wider than intervening grooves and bend laterally; ribs becoming irregular, but not broken into pustules near lateral triangle; longitudinal ribs of jugum fine, close-packed, directed anteriorly; lateral triangle with broad, slightly oblique, concentric ribs; insertion plate with one slit per side. Posterior valve with central mucro; central areas with sculpture like that of intermediate valves; posterior slope with sculpture of lateral triangle, but slightly more irregular; insertion plate with 8–11 slits.

Girdle scales 120–150 μm high, about 95 μm wide; 15–

Description: Animal reaching a length of 45 mm, elongate. Color variable with pink or green predominating;

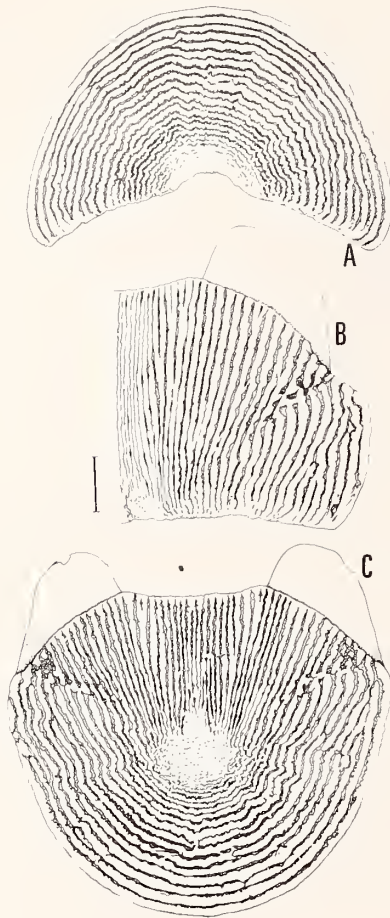


Figure 10

Stenoplax purpurascens (C. B. Adams). North side of Galeta Id., Panama (RCB). A, anterior valve. B, right portion of intermediate valve. C, posterior valve. Scale bar = 1 mm.

23 ribs per scale; ribs may or may not reach apex. Girdle fringe with straight, ribbed spicules approximately $97\ \mu\text{m}$ long.

Radula typical for subgenus. Denticle cap of major lateral tooth tricuspidate, moderately squat; small cusp pronounced; all cusps blunt; brown basal spot present.

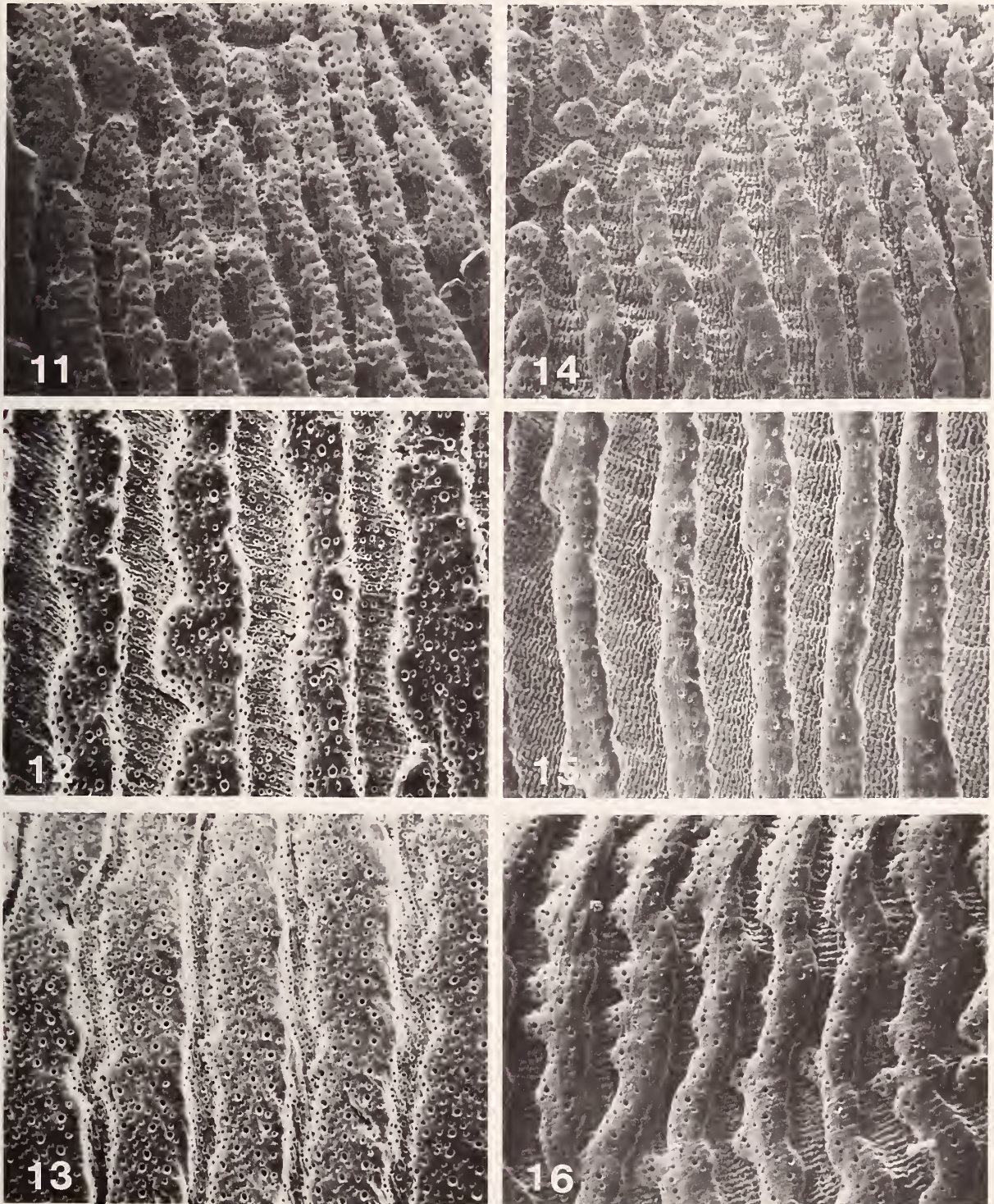
Remarks: There is much confusion in the literature about the relationship between the eastern Pacific *S. limaciformis* and the West Indian *S. purpurascens*. Sowerby's specimens were from Inner Lobos Island, Peru, and Guacomayo [southern Chiapas, Mexico, *vide* KEEN (1971)]. The general description given by Sowerby (*in* BRODERIP & SOWERBY, 1832) and the lack of specimens in museum collections certainly contributed to taxonomic chaos. DALL (1889) and PILSBRY (1892:57) both used Sowerby's name for the western Atlantic species that is herein recognized

as *S. purpurascens*. Pilsbry concluded that "the West Indian specimens collected by Robert Swift at St. Thomas and the Peruvian specimens which I have examined are absolutely identical in character . . ." THIELE (1909, 1910a) studied shell and girdle scale morphology of these species and he concluded that the West Indian species is not conspecific with *S. limaciformis*. Thiele's work, however, was ignored by American authors who continued to follow Pilsbry. ABBOTT (1954), KEEN (1958), and Thorpe (*in* KEEN, 1971), for example, all stated that *S. limaciformis* occurs in the Caribbean. KAAS (1972), who noted "rather striking differences between the two species," corroborated Thiele's earlier findings and he used the name *Ischnochiton purpurascens* (C. B. Adams) for the West Indian species. The culmination of this confusion is seen in ABBOTT's (1974) second edition of *American Seashells* in which he recorded both *S. limaciformis* and *S. purpurascens* from the western Atlantic.

FERREIRA (1978) was the first person to study large samples of New World *Stenoplax* from various localities. In his report on the status of the polyplacophoran species described from Jamaica by C. B. Adams, Ferreira examined the West Indian "*limaciformis*" problem in some detail. He concluded that differences in shell, girdle, and radular features do not warrant the use of the names *S. floridana* or *S. purpurascens*. FERREIRA (1978:88) found "many intergradations in the described tegmental sculptures, and many forms of transition between '*floridanus*' and '*limaciformis*' often in specimens found side by side at the same collection station." At the time Ferreira published his results, I was just beginning to examine *Stenoplax* specimens from Honduras and the Caribbean coast of Panama. I did not immediately see intergradations between *S. floridana* and *S. purpurascens*, and I therefore began a study that would allow me to decide independently the status of these *nomina*. My investigation began by using scanning electron microscopy to obtain high magnification photographs of the dorsal shell sculpture. Other parts of the investigation were devoted to an examination of the girdle elements and radulae using light microscopy.

I have concluded that *Stenoplax limaciformis*, *S. purpurascens*, and *S. floridana* are closely related but specifically distinct; furthermore, a third Caribbean species, *S. producta* (Reeve, 1847), exists. I can state that the reason that FERREIRA (1978) found differing entities "side by side at the same collecting station" is that each different western Atlantic species occurs sympatrically with another member of the group over a part of its range. Light microscopy of shell features, especially using glistening, alcohol-preserved specimens, can lead to confusion. But SEM studies of the shell and a study of denticle cap morphology have allowed the recognition of the subtle differences that characterize each member of this group of sibling species. Knowledge of these differences readily allows one to identify the species using a dissecting microscope.

Stenoplax purpurascens is more closely related to the eastern Pacific *S. limaciformis* than to *S. floridana* or *S.*



Explanation of Figures 11 to 16

Scanning electron micrographs of intermediate valve sculpture of *Stenoplax purpurascens* (C. B. Adams) and *S. producta* (Reeve). Posterior side toward top of page; all photographs 186 \times . Figures 11 to 13: *S. purpurascens*, Porto Bello, Panama (RCB). Figures 14 to 16: *S. producta*, Nassau, New Providence Id., Bahama Islands (GTW).

Figures 11, 14. Posterior region of central area near lateral triangle. Note the tendency for the ribs of *S. producta* to break into pustules near the lateral triangle, and the furrowlike sculpture in the intervening grooves.

Figures 12, 15. Central area near anterior margin. Note the low density of esthete pores on the ribs of *S. producta*.

Figures 13, 16. Lateral triangle.

Table 1

Esthete pore density and rib area measurements of members of the *Stenoplax limaciformis* species complex. All figures \pm SD. "Total" numbers derived from mean of each individual. See text for further explanations.

		\bar{x} SDEN/mm ²	\bar{x} LDEN/mm ²	\bar{x} TOTDEN/mm ²	\bar{x} PCTRA
<i>S. limaciformis</i> (n = 13)	TC	6348 \pm 1210	1388 \pm 299	7736 \pm 1369	59.4 \pm 6.6
	AM	5349 \pm 949	1248 \pm 162	6597 \pm 996	56.0 \pm 8.5
	LT	6383 \pm 1151	2086 \pm 305	8469 \pm 1306	68.8 \pm 6.2
	Total	6021 \pm 984	1611 \pm 223	7633 \pm 1123	61.5 \pm 6.1
<i>S. purpurascens</i> (n = 11)	TC	6798 \pm 1177	1278 \pm 128	8075 \pm 1222	68.9 \pm 7.1
	AM	5872 \pm 652	1166 \pm 157	7037 \pm 678	69.9 \pm 8.2
	LT	7505 \pm 1166	2089 \pm 422	9494 \pm 1286	75.5 \pm 5.9
	Total	6753 \pm 609	1524 \pm 166	8277 \pm 685	71.5 \pm 4.8
<i>S. floridana</i> (n = 11)	TC	4821 \pm 636	949 \pm 137	5770 \pm 752	47.9 \pm 7.6
	AM	2690 \pm 843	566 \pm 128	3257 \pm 898	43.5 \pm 6.4
	LT	5499 \pm 862	1119 \pm 239	6618 \pm 1051	54.8 \pm 4.3
	Total	4405 \pm 719	894 \pm 163	5300 \pm 832	48.6 \pm 4.4
<i>S. producta</i> (n = 6)	TC	3706 \pm 869	904 \pm 114	4610 \pm 962	56.4 \pm 3.4
	AM	2348 \pm 1144	512 \pm 118	2860 \pm 1260	56.6 \pm 7.4
	LT	5037 \pm 1215	1155 \pm 139	6192 \pm 1326	64.7 \pm 9.7
	Total	3790 \pm 1013	875 \pm 118	4665 \pm 1121	59.3 \pm 5.0

producta with which it occurs sympatrically over parts of its range. Both *S. purpurascens* and *S. limaciformis* have a centrally located mucro on the posterior valve and ribs on the central areas that do not form pustules near the lateral triangle. In addition, these ribs are broader and they have a much higher density of esthete pores than in *S. producta* and, especially, *S. floridana* (Table 1). The broadness of the ribs may be quantified by the area of the valve (as a percent) covered by ribs (PCTRA; see Table 1). All species except *S. floridana* have more than 50% of the intermediate valve covered by ribs; *S. purpurascens* has much higher values for PCTRA than the other species. Canonical variate analysis using the density of the megalopores (LDEN) and percent rib area (PCTRA) as variables reveals that two groups of the *S. limaciformis* species complex exist: one group is composed of *S. limaciformis* and *S. purpur-*

ascens while the other group consists of *S. floridana* and *S. producta*. The Mahalanobis D² distances, which reflect the distance between the centroids of each species, are much greater between these two groups than within each group (Table 2).

Both *Stenoplax limaciformis* and *S. purpurascens* have a brown basal spot on the denticle cap of the major lateral tooth. The denticle cap of *S. purpurascens* differs considerably by lacking the bulging outline along the side with the small cusp, and the small cusp is more prominent (Figures 8E, F). The species also differ in the sculpture of the lateral triangle, the anterior valve, and the posterior slope of the posterior valve. In *S. purpurascens* this sculpture typically is of rather flat, wavy, concentric ribs, whereas in *S. limaciformis* there is a much greater tendency for these ribs to be broken into broad nodules, especially on the end valves.

When compared with the other Caribbean species, *Stenoplax purpurascens* differs by its central, not posteriorly acentric, mucro on the posterior valve, and by wavy concentric ribs on the anterior valve. In both *S. floridana* and *S. producta* the anterior valve is granular, although some specimens of the latter species from 18 m at Gold Rock, Grand Bahama Island (FDNR 30416) interestingly differ in this respect and exhibit concentric sculpture. The lateral triangle of *S. producta* has concentric ribs, as does *S. purpurascens*, but the ribs in the former are typically more narrow, and they are parallel to the antero-posterior axis, rather than slightly oblique to it. The characteristic furrowlike sculpture in the grooves of *S. producta* (Figures 14-16), visible under high magnification in non-eroded specimens, serves to differentiate the species from

Table 2

Mahalanobis D² distance values between members of the *Stenoplax limaciformis* species complex. The distance values are in the upper triangle and probability values in the lower triangle. LIM = *S. limaciformis*, PUR = *S. purpurascens*, FLO = *S. floridana*, PRO = *S. producta*. See text for further explanations.

Species	LIM	PUR	FLO	PRO
LIM	—	1.94	5.89	4.61
PUR	<0.001	—	7.14	5.41
FLO	<0.001	<0.001	—	2.19
PRO	<0.001	<0.001	<0.05	—

S. purpurascens and other *Stenoplax* s.s. Both *S. floridana* and *S. producta* have a more elongate denticle cap on the major lateral tooth, the two larger cusps are more pronounced, and the brown basal spot, seen in *S. purpurascens*, is absent (Figures 8C, D, G, H).

FERREIRA (1978) mentioned that he had observed "many forms of transition" between members of the Caribbean *limaciformis* group. He did not state the localities where he had observed this phenomenon, but it is likely that he had encountered examples of either *Stenoplax producta*, which previous authors have not recognized, or some of the interesting intraspecific variation exhibited by *S. floridana*. *Stenoplax purpurascens* occurs sympatrically with *S. floridana* in the southern Caribbean (Panama and Colombia); it lives with *S. producta* in Cuba, Hispaniola, and Jamaica. In these cases I did not observe any intergradation; the shell sculpture indicated one species or the other, and these conclusions were consistently supported by SEM analysis of valve microsculpture and light microscopic observation of the radula.

Distribution: *Stenoplax purpurascens* occurs from Cuba and Hispaniola south and east through the Caribbean to Panama, the northern coast of South America, and Brazil (Figure 9A).

Specimens examined: *Cuba:* Gibara; Santiago (both GTW).—*Jamaica:* Montego Bay (MCZ); 2 mi (3.2 km) W of Runaway Bay, 1–1.5 m; along seawall, just W of Runaway Bay, 0.15–1 m (both RCB); Port Henderson (GTW).—*Haiti:* Miragoâne (MCZ).—*Dominican Republic:* Santa Bárbara de Samaná (MCZ); small cove just E of Embassy Beach, 16 km E of Boca Chica, 0.5–2 m; Isla La Matica, Playa Boca Chica, 0.5–1 m (both RCB).—*Puerto Rico:* Phosphorescent Bay; Magueyes Id., La Parguera; Cayo Enrique, La Parguera (all RCB); Arrecife Media Luna 2.25 mi (3.6 km) S of La Parguera (MCZ); Cabo Rojo Lighthouse (RCB); Playa Sucia, Cabo Rojo (MCZ).—*Virgin Islands:* Water Id., St. Thomas; St. Croix (both GTW); The Bight, Norman Id., 1–5 ft (0.3–1.5 m) (MCZ).—*Antigua:* Falmouth Harbour; Hawkes Bill Bay (both RCB).—*St. Lucia:* Vieux Fort (MCZ).—*Barbados:* Archers Bay, St. Lucy; Bridgetown (both RCB).—*Tobago:* (MCZ).—*Trinidad:* Maguaripe Beach, 1.5–3 m (RCB).—*Aruba:* Commanders Bay (RCB).—*Panama:* Toro Pt., ocean side (RCB); Galeta Id. (GTW, RCB); Reef off Cocal Pt., Porto Bello; Porto Bello (both RCB).—*Venezuela:* Cayo Punta Brava, Parque Nacional de Morrocoy, Tucacas (RCB).

Stenoplax floridana (Pilsbry, 1892)

(Figures 8G, H, 9B, 17–23)

Ischnochiton (Stenoplax) limaciformis (Sowerby). DALL, 1889: 415 [in part]. *Non Stenoplax limaciformis* (Sowerby).

Ischnochiton (Stenoplax) floridanus PILSBRY, 1892:58, pl. 17, figs. 19–22 (Key West, Florida; holotype ANSP 35694).

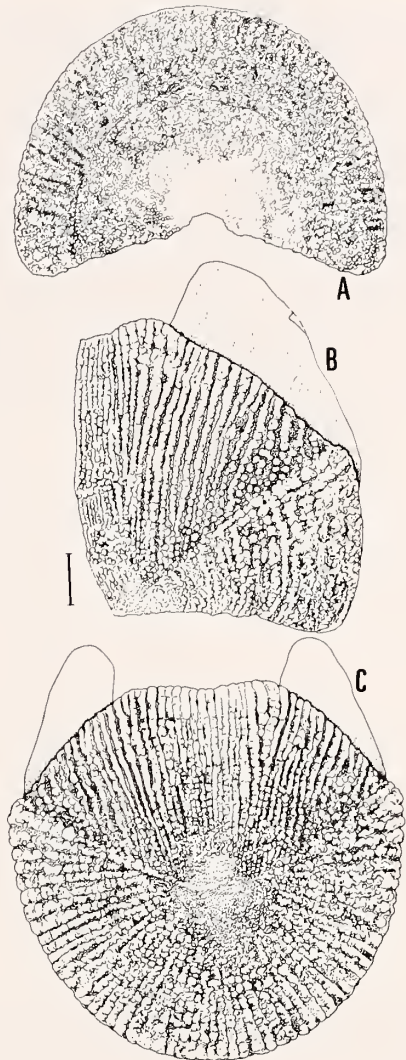


Figure 17

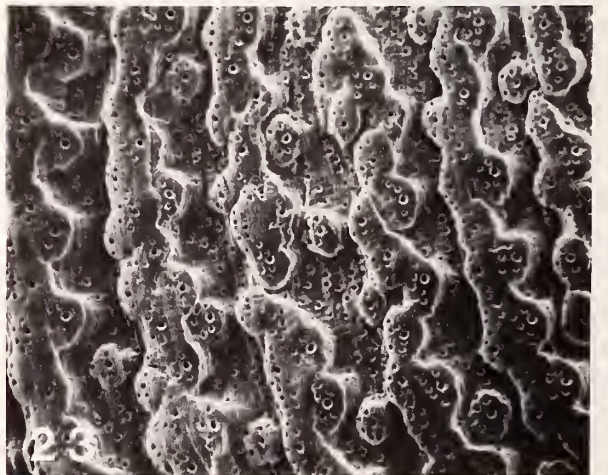
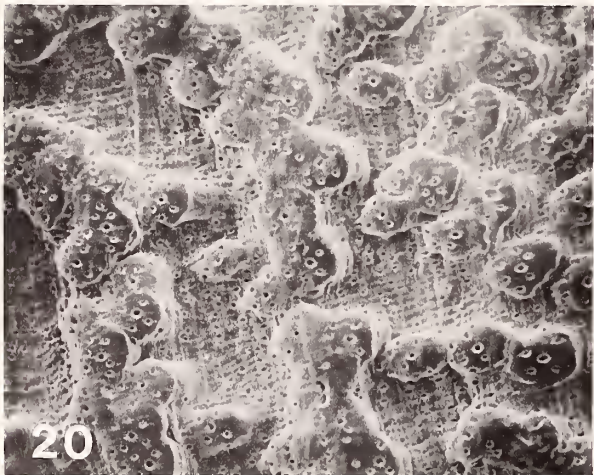
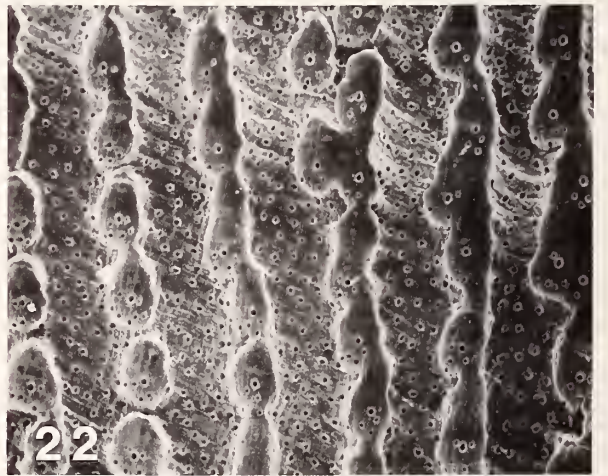
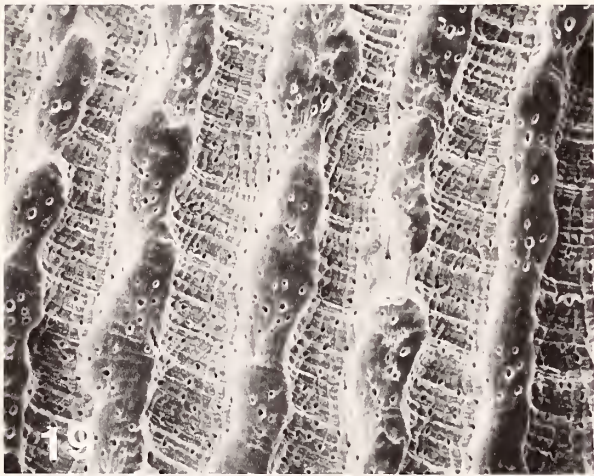
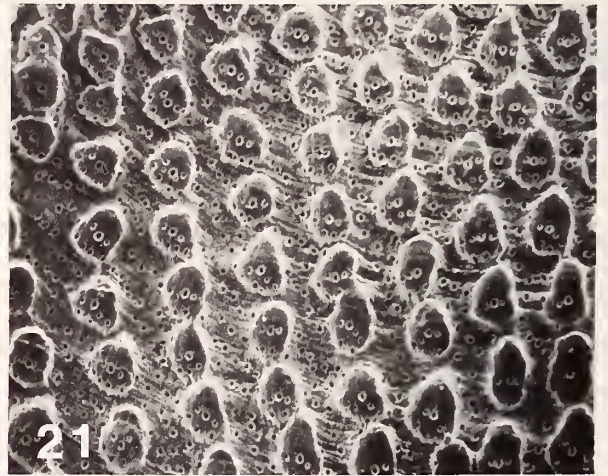
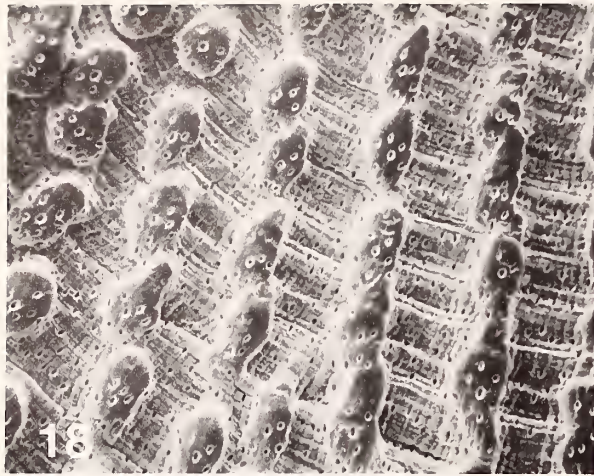
Stenoplax floridana (Pilsbry). Just north of Crawl Key, Florida Keys, Florida (RCB). A, anterior valve. B, right portion of intermediate valve. C, posterior valve. Scale bar = 1 mm.

Ischnochiton floridanus Pilsbry. JOHNSON, 1934:13; ABBOTT, 1954:320; GÖTTING, 1973:248, pl. 9, fig. 5.

Stenoplax floridana (Pilsbry). ABBOTT, 1974:396, fig. 4653; EMERSON & JACOBSON, 1976:464; TURGEON & LYONS, 1977:88; KAAS & VAN BELLE, 1980:48.

Stenoplax limaciformis (Sowerby). FERREIRA, 1978 [in part]: 87.

Description: Animal reaching a length of 50 mm, elongate. Color highly variable, but typically cream white with small dark green speckles. Anterior valve granular; small nodules may be radially or concentrically arranged, depending on growth lines; insertion plate with 8–11 slits. Intermediate valves moderately inflated, angular; longi-



Explanation of Figures 18 to 23

Scanning electron micrographs of intermediate valve sculpture of *Stenoplax floridana* (Pilsbry). Posterior side toward top of page; all photographs 186 \times . Figures 18 to 20: Indian Key Fill, Florida Keys, Florida (RCB). Figures 21 to 23: North side of Galeta Id., Panama (RCB).

Figures 18, 21. Posterior region of central area near lateral triangle. Note that the ribs are conspicuously broken into pustules, the sparseness of esthete pores on the ribs and pustules, and the lack of pronounced sculpture in the intervening grooves.

Figures 19, 22. Central area near lateral triangle.

Figures 20, 23. Lateral triangle.

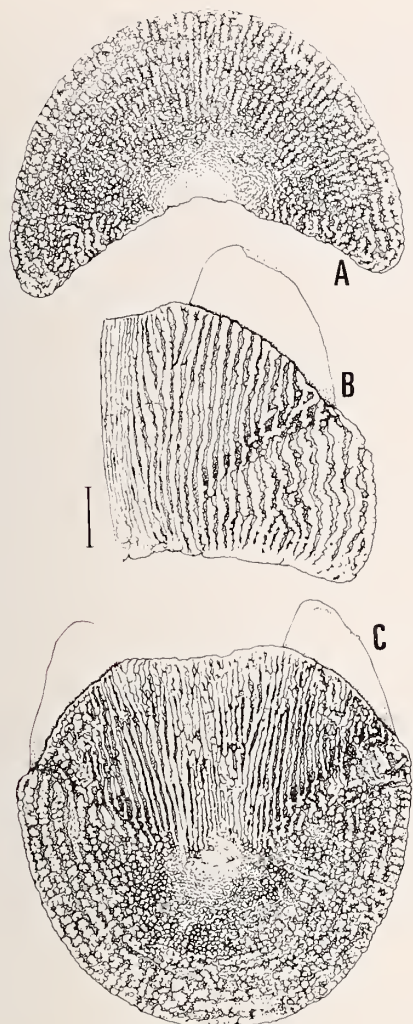


Figure 24

Stenoplax producta (Reeve). Arthur's Town, Cat Id., Bahama Islands (MCZ 279211). A, anterior valve. B, right side of intermediate valve. C, posterior valve. Scale bar = 1 mm.

tudinal ribs of jugum fine, directed anteriorly; ribs of central areas typically not as wide as intervening grooves, directed laterally; ribs broken into ovate to round pustules near lateral triangle; insertion plate with one slit per side. Lateral triangle sharply raised, with numerous small nodules which may be radially arranged or appear to be concentrically arranged due to heavy growth lines or slight coalescing of nodules. Posterior valve elongate; mucro posteriorly acentric; jugal area reduced; central area sculpture as in intermediate valves; posterior slope sculpture as in anterior valve; insertion plate with 8–12 slits.

Girdle scales about 100–125 μm long, 77–93 μm wide, 9–13 ribs per scale; ribs reach apex in some populations but conspicuously do not in other populations. Girdle fringe with straight, ribbed spicules 77–89 μm in length.

Radula typical for subgenus. Denticle cap of major lateral tooth tricuspidate, rather elongate; small cusp pronounced, all cusps pointed; outline of side with small cusp often quite straight occasionally inwardly curved; brown basal spot absent (Figures 8G, H).

Remarks: *Stenoplax floridana* is the most easily distinguished member of the *S. limaciformis* group. The consistent break-up of the longitudinal ribs of the central area near the lateral triangle into pustules allows instant recognition. The valve surface of *S. floridana* has much less surface area covered by ribs than the other species (Table 1). This reduction is due not only to the narrowness of the ribs but to the break-up of the ribs into pustules in the top central (TC) and lateral triangle (LT) areas. Although the ribs of *S. floridana* have a lower density of esthete pores than *S. limaciformis* or *S. purpurascens*, the density is higher than that observed in *S. producta*.

Long thought to be restricted to the Florida Keys, the species extends southward to the northern coast of Colombia (GÖTTING, 1973). *Stenoplax floridana* differs from *S. purpurascens*, with which it occurs sympatrically along the Caribbean coast of Panama and Colombia, by its more sharply raised lateral triangle which is granular, not with broad concentric ribs. Also, *S. purpurascens* never exhibits a break-up of the central area ribs into pustules. The denticle cap of the two species differs considerably: in *S. floridana* the denticle cap is more elongate, and an outline of the cap usually shows a straight side below the small cusp; the cusps of *S. floridana* are more pronounced and more pointed than those of *S. purpurascens* (Figures 8G, H). *Stenoplax floridana* lacks the brown basal spot of the denticle cap that is so characteristic of *S. purpurascens* and *S. limaciformis*. Some authors have noted that the girdle scales of the two species may be used as a differentiating character (PILSBRY, 1892; THIELE, 1910a; KAAS, 1972). There seems to be much intraspecific variation, often expressed on a geographic basis, in girdle scale morphology. Early in my investigation when I had sampled the scales of only a few individuals, I had also concluded that the girdle scales were taxonomically useful, but I now feel that statements concerning girdle scale differences must be made with caution. Scales of typical *S. floridana* from the Florida Keys have fewer ribs (9–12) than West Indian *S. purpurascens* (15–18); I never observed a rib count as low as that stated by KAAS (1972) who found 8 ribs. In the Florida Keys the ribs do not reach the apex, as Kaas noted, but this feature is certainly not true for populations of *S. floridana* from Honduras and Panama. Similarly, the girdle scales in some populations of *S. purpurascens* have ribs that do not reach the apex while other populations differ in this respect.

Stenoplax floridana is most likely to be confused with the previously overlooked *S. producta* (Reeve). Usually both species have a granular anterior valve and both often have thin ribs on the central areas; in *S. producta* these ribs occasionally show a slight break-up into pustules, but pustular formation is minimal. The lateral triangle of *S.*

producta has well developed concentric ribs whereas in *S. floridana* the lateral triangle is granular with the granules sometimes coalescing to form nodular radial ribs. In some specimens from Dry Tortugas and Key Largo, the granules partially coalesce to form irregular concentric ribs. Also, while some *S. floridana* have faint microscopic furrows in the intervening grooves, this feature is highly exaggerated in *S. producta*. The radular denticle cap of the two species differs considerably: in *S. floridana* the small cusp is pronounced and the remaining two cusps are elongated and pointed, whereas in *S. producta* the small cusp is often reduced and the other two cusps are broad and blunt (Figures 8C, D, G, H).

Distribution: *Stenoplax floridana* occurs from the offshore waters of the western coast of Florida to the Florida Keys and south to Honduras, Panama, and Colombia. The record from Nassau in the Bahama Islands has not been confirmed by recent collecting and it may be in error (Figure 9B).

Specimens examined: *Bahama Islands:* Nassau, New Providence Island (GTW).—*Florida:* Biscayne Bay (MCZ); Virginia Key; Old Spanish Light, Biscayne Bay (both GTW); Soldier Key (RCB); Ragged Keys (GTW, MCZ); Elliott Key (MCZ); Just E of Card Sound Bridge, Key Largo (RCB); Tavenier Key; Windley Key (both GTW); Tea Table Key; Indian Key Fill (both RCB); Indian Key (MCZ); Long Key, bay side (RCB); Conch Key; Grassy Key (both GTW); just N of Crawl Key (RCB); Crawl Key, bay side; Old Ferry Dock, Crawl Key; Bay Point, Crawl Key (all MCZ); Bonefish Key (GTW, MCZ); Pigeon Key (MCZ); Little Duck Key (GTW, RCB); Missouri Key (GTW, MCZ, RCB); Bahia Honda (GTW); West Summerland Key (RCB); Little Torch Key (MCZ); Pelican Shoals; Sambo Shoals (both GTW); Boca Chica (MCZ); Key West (GTW, MCZ); Long Key Reef, Dry Tortugas; N and E side of Bush Key, Dry Tortugas, 2–4 m; W side of Ft. Jefferson, Garden Key, 1–2 m; near moat wall, W side of Garden Key, Dry Tortugas, 0–2 m; SW corner of Garden Key, Dry Tortugas, 1.5–2 m; Bird Key Reef, Dry Tortugas, 0.5–1 m (all FDNR); BLM Sta. 151, 28°32'6"N, 084°18'54"W, 80–90 ft (24–27 m); BLM Sta. 047, 28°34'N, 084°20'12"W, 85–95 ft (26–28 m); BLM Sta. 251, 28°32'54"N, 084°6'24"W, 80–90 ft (24–27 m); BLM Sta. 247, 28°36'18"N, 084°9'42"W, 80–90 ft (24–27 m); BLM Sta. 146, 28°41'N, 084°23'18"W, 80–90 ft (24–27 m) (all approximately 110 mi [176 km] S of St. Marks, all DISL).—*Honduras:* Anthonys Key, Roatán Id. (RCB).—*Panama:* Galeta Id. (GTW, RCB); Verde Id., Mantilla Pt., Porto Bello (RCB).

Stenoplax producta (Reeve, 1847)

(Figures 8C, D, 9C, 14–16, 24)

Chiton productus REEVE, 1847:pl. 17, sp. 97 (Locality unknown [herein designated to be Eight Mile Rock, Grand Bahama Island]; holotype in BMNH).

Ischnochiton (Stenoplax) limaciformis (Sowerby). BOONE, 1933: 199, pl. 125, fig. A. *Non Stenoplax limaciformis* (Sowerby).

Stenoplax limaciformis (Sowerby). LYONS, 1981:38 (list). *Non Stenoplax limaciformis* (Sowerby).

Non Chiton productus 'Reeve' THIELE, 1909:7; 1910a:80; 1910b:110 [= *Stenoplax purpurascens* (C. B. Adams)].

Description: Animal reaching a length of about 30 mm, elongate. Color variable but usually speckled with green and white; slight rusty tinge often seen. Anterior valve usually granular; granules radially or concentrically arranged, depending on growth lines; insertion plate with 8–12 slits. Intermediate valves with fine longitudinal ribs on broad jugum; central areas with slightly flattened longitudinal ribs that are directed laterally; ribs almost as wide or wider than intervening grooves; ribs become irregular, but rarely break into a few pustules near lateral triangle; lateral triangle often sharply raised, with concentric ribs directed along antero-posterior axis; insertion plate with one slit per side. Grooves of lateral triangle and central areas with very fine furrowlike riblets visible at high magnification. Posterior valve elongate, mucro posteriorly acentric; jugal and central areas as in intermediate valves; posterior slope as in anterior valve, insertion plate with 8–11 slits.

Girdle scales about 118 μ m high, 76–97 μ m wide; 12–18 ribs per scale; ribs do not reach apex. Girdle fringe with straight, narrow spicules about 126 μ m long, 14 μ m wide.

Radula typical for subgenus. Denticle cap of major lateral tooth tricuspidate, rather elongate, small cusp somewhat reduced to nearly absent; two large cusps prominent, blunt; brown basal spot absent; elongate, V-shaped "tear" often present at base (Figures 8C, D).

Remarks: *Stenoplax producta* has remained unrecognized since its introduction by REEVE (1847). Although the locality of this species was unknown, most authors have listed the name in synonymy with *S. limaciformis* (Sowerby, 1832). After examination of the figures presented by Reeve, especially the "detail of sculpture" figure at the back of his work, and color and black-and-white photographs I made of the unique type specimen present in the British Museum (Natural History), I have concluded that Reeve's species is the Caribbean *Stenoplax* that one finds so commonly in the Bahama Islands. I herein designate Eight Mile Rock, Grand Bahama Island, as the type locality of *S. producta*. The type specimen exhibits concentric ribs on the lateral triangle that are directed along the longitudinal axis and not directed slightly obliquely as one sees in *S. purpurascens*, and the elongate posterior valve has a posteriorly acentric mucro. REEVE (1847: *Chiton* pl. 17, sp. 97) also seemed aware of the narrow ribs of his new species: he noted that the central areas were "longitudinally grooved" [stress on grooves]; in the next species listed, *Chiton sanguineus* [= *S. purpurascens*], he stated that the central areas were "very closely longitudinally striated" [stress on ribs]. All of these features lead one to recognize *S. producta* as the "Bahamian" *Stenoplax*.

REEVE's (1847) statements and illustrations do not completely agree with the British Museum specimen. Reeve clearly figures concentric ribs on the posterior slope of the posterior valve, and in the description he stated "terminal valves and lateral areas of the rest concentrically undulately striated." Although this statement is true for lateral triangle sculpture, the posterior slope of the single type specimen has a rather granular appearance due to a combination of radial and concentric arrangement of the granules. Whether Reeve for brevity's sake stressed "concentric," or whether the specimen Reeve described is no longer present in the type lot, is uncertain. Although *Stenoplax producta* typically has very granular areas on the anterior and posterior valves, it also can have wavy concentric ribs, as the specimens from Gold Rock, Grand Bahama Island attest (FDNR 30416).

There seems to be no doubt that *Stenoplax producta* is more closely related to *S. floridana* than to *S. limaciformis* or *S. purpurascens*. The denticle cap of the major lateral tooth of *S. producta* most closely resembles that of *S. floridana* and both types lack the brown basal spot observed on the denticle caps of *S. limaciformis* and *S. purpurascens* (Figure 8). Both *S. producta* and *S. floridana* have considerably fewer esthete pores, and a higher percentage of the valve surface is taken up by ribs, although in this respect *S. producta* is much more similar to *S. limaciformis* and *S. purpurascens* than to *S. floridana* (Table 1). Canonical variate analysis using the density of megalopores (LDEN) and percent rib area (PCTRA) indicates that *S. producta* forms a natural group with *S. floridana*; the Mahalanobis D^2 distance value is low when *S. producta* and *S. floridana* are compared, and high when *S. producta* is contrasted with the other two species (Table 2).

Distribution: *Stenoplax producta* ranges from the Bahama Islands and the offshore reef areas of the Florida Keys south to Cuba, Hispaniola, Jamaica, Honduras, and Isla de San Andrés (Figure 9C).

Specimens examined: *Florida:* Ragged Rocks (GTW); Looe Key (MCZ); Pelican Shoals (GTW); Sand Key, S of Key West, 0.5–2 m; Long Key Reef, Dry Tortugas; patch reef near Long Key Reef, Dry Tortugas, 1.5–2.5 m; N and E side of Bush Key, Dry Tortugas, 2–4 m; W side of Ft. Jefferson, Garden Key, Dry Tortugas, 1–2 m; SW corner of Garden Key, Dry Tortugas, 1.5–2 m; near moat wall, W side of Garden Key, Dry Tortugas, 0–2 m; Bird Key Reef, Dry Tortugas, 0.5–1 m; W side of Loggerhead Key, Dry Tortugas, 0–1 m (all FDNR).—*Bahama Islands:* *Grand Bahama Island:* Settlement Point, West End, 0–2 m; Sports Dock, West End, 0.5–1.5 m (both FDNR); shallow cove, 2 mi (3.2 km) W of Eight Mile Rock, 0–0.5 m; Eight Mile Rock, 1–2 m (both RCB); pool at entrance to underwater cave, E of Eight Mile Rock, 0.5–1 m (FDNR,RCB); W side of jetty, W of entrance to Freeport Harbour, 2–3 m (RCB); Jetty and adjacent bar, Caravel Beach, Freeport, 0–1.5 m; Gold Rock, 18 m; Deadman's Reef, 0.5–1.5 m; McLean's Town, East End, 1–2 m (all FDNR); *Bimini Islands:* Bimini

(GTW); North Lagoon, E coast of North Bimini (FMNH); Gun Cay, Bimini (MCZ); *Eleuthera Island:* Harbour Id. (GTW); Sand Pt., Savanna Sound (MCZ); *New Providence Island:* Nassau (GTW); Eastern Point; Fox Hill, South Beach (both MCZ); E of Clifton Pier, 1–2 m; Clifton Bluff, 4 m; Clifton Pt., 0–2 m (all RCB); *Cat Island:* Arthur's Town (MCZ); *Long Island:* Clarence Town (MCZ).—*Cuba:* Varadero (GTW).—*Jamaica:* 2 mi (3.2 km) W of Runaway Bay, 1–1.5 m; along seawall, just W of Runaway Bay, 0.5–1 m (both RCB).—*Haiti:* Gonâve Id.; Miragoâne (both MCZ).—*Dominican Republic:* Isla La Matica, Playa Boca Chica, 0.5–1 m (RCB).—*Isla de San Andrés:* Paradise Pt. (RCB).—*Honduras:* Anthonys Key, Roatán (RCB).

DISCUSSION

According to MAYR (1969:411), sibling species are "pairs or groups of closely related species which are reproductively isolated but morphologically identical or nearly so." The different species of the *Stenoplax limaciformis* complex are certainly very similar in appearance and the question that then remains is the determination of reproductive isolation. If the Caribbean species were geographically present as entirely allopatric groups of populations, which they are not, it might be convenient for some taxonomists, given the lack of major morphological differences, to assume that reproductive isolation had not been achieved and to view them as subspecies. But as WILEY (1981) noted, this approach, which is based on the view that species status has not been tested by sympatry, would lead to confusion. In the present paper it is shown that over part of its range each Caribbean species occurs sympatrically with another member of the group. *Stenoplax purpurascens* occurs with *S. producta* in Cuba, Hispaniola, and Jamaica; it is found with *S. floridana* in Panama and Colombia. *Stenoplax floridana* lives with *S. producta* on the offshore reefs of the Florida Keys and Roatán Island, Honduras. The fact that no hybrid zones are evident where sympatry occurs is conclusive proof that speciation has occurred. The allopatric *S. limaciformis* from the eastern Pacific must be considered specifically distinct from Caribbean members. It is as different from Caribbean members as the Caribbean members are from each other. It must be stressed that the small, but consistent, morphological differences observed among members of the *Stenoplax limaciformis* species complex strongly support the argument that species status has been achieved in each case.

The lack of biological information about *Stenoplax s.s.*, and chitons in general, prohibits any definitive statements about the restricted distribution of these species within the West Indian faunal province. The distributional pattern of members of the *S. limaciformis* complex in the West Indies, however, does suggest that their larvae remain planktonic for only a brief period. If this were not so one would expect broader distributional patterns within the West Indian province. The only report in the literature pertaining to the embryogeny of *Stenoplax* is that of HEATH

(1899) who reported that in *Stenoplax* (*Stenoradsia*) *heathiana* Berry, 1946, settlement of the larvae occurs during a period of 15 minutes to three hours after they become free swimming. A relatively short, but not as brief, planktonic existence is found in various other polyplacophorans (PEARSE, 1979). *Stenoplax purpurascens* occurs throughout the West Indies, yet it is conspicuously absent in the Bahama Islands and the Florida Keys. Its erroneously reported presence in Bermuda (CROZIER, 1920; ABBOTT, 1974) is based on specimens of *Stenoplax boogi* (Haddon, 1886). *Stenoplax floridana*, so abundant in the Florida Keys, is apparently lacking in the Bahama Islands, and *S. producta*, which is widely distributed in the western Caribbean, is commonly found at Dry Tortugas and offshore reefs of the Florida Keys, but not in the lower Florida Keys proper. It is likely that the Gulf Stream is a major disrupting force in the distribution of *Stenoplax*, not counting the fact that the distances involved, such as between Florida and the Bahama Islands, might be a sufficiently great barrier even if current patterns were more favorable.

Given the restricted distribution of *Stenoplax s.s.* within the West Indian faunal province, it would seem that the species might provide additional evidence for the theory of paraprovincialism as applied to the Caribbean (PETUCH, 1982). *Stenoplax floridana* and *S. producta* have a distributional pattern that reflects a Caloosahatchian origin, while the range of *S. purpurascens* indicates a Gatunian origin. The general current pattern in the Caribbean, which is from east to west, has probably kept *Stenoplax* species from extending their range eastward except for along continental margins; but even along continental shores large regions of mangrove and muddy substrates could prove to be an effective barrier. Thus, *S. floridana* and *S. producta* have probably been restricted to the western Caribbean and only *S. purpurascens* exists in the Lesser Antilles. *Stenoplax limaciformis* is the only species of the *S. limaciformis* group that is found in the eastern Pacific due to the continuous continental margin and the lack of insular environments. Shell and radular morphology of *S. limaciformis* are quite uniform throughout its extended range. It is lacking in offshore island groups, such as the Revillagigedo Archipelago (FERREIRA, 1983), Cocos Island (HERTLEIN, 1963), and the Galápagos Islands (SMITH & FERREIRA, 1977), which possess a fairly typical Panamic fauna.

Specific comments on the evolutionary relationships among the species of New World *Stenoplax s.s.* must await additional material. Adequate samples from the western Caribbean are especially lacking, but evidence available to date indicates that the *S. limaciformis* complex is composed of two distinct groups. The first group, whose members include *S. floridana* and *S. producta*, forms a lineage characterized by reduced rib width, fewer esthetes, and an elongate denticle cap. The second group, which includes *S. purpurascens* and *S. limaciformis*, has wide ribs, many esthete pores, and a rather squat denticle cap. These conclusions have been drawn from general observations of shell and radular morphology. The results of SEM anal-

ysis of valve microsculpture, especially the extent of rib surface area and the density of megalesthete pores, have provided corroborating evidence.

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